The Effect of Species Composition on the Survival of Mixed Populations of the Sea Mussels *Mytilus californianus* and *Mytilus edulis*

BY

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(5 Text figures)

In the course of an investigation into the nature of competitive interaction between the sea mussels *Mytilus californianus* Conrad, 1837 and *M. edulis* Linnaeus, 1758 on the coast of Southern California (Santa Barbara) (Harger, 1968), it became apparent that the immediate outcome of such an interaction depended in large part on the ratio of the two species concerned.

Several authors in the past have envisaged situations wherein the coexistence of ecological homologues would be permitted. For instance, Hutchinson (1957) claims that coexistence might occur if the advantage of one species over the other is constantly reversed by habitat variations; however, Klomp (1961) considers that this could occur only if habitat variations were dependent on the numerical ratio of the species involved, and this seems improbable.

It is proposed that within this system of interacting mussels inhabiting the intertidal region at least one effect of environmental variation is directly dependent on the numerical ratio of the species involved and that furthermore, the advantage possessed by each species over the other may be reversed by habitat variations (e. g. *Mytilus edulis* may be washed off by heavy seas, thus permitting formerly imprisoned *M. californianus* to grow. A period of calm weather may permit re-domination by *M. edulis*).

This paper deals with the effect of a physical environmental variable (wave action) on the survival of mixed populations of mussels.

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METHODS

a. Relationship of Mussel Size to Environmental Conditions

Mussel clumps growing in intertidal beds on the shore adjacent to Ellwood Pier, 14 miles north of Santa Barbara, during 1964 - 1967 were composed principally of *Mytilus californianus*; individuals of *M. edulis* occurring there were quite small, usually between 2 and 4 cm in length (measured between the umbo and siphon regions), whereas *M. californianus* sometimes attained a length of up to 20 cm. The shore itself is gently sloping, containing large projecting boulders in some places and extensive lines of slanting reefs in others. The situation here differed markedly from the pier (see Harger, 1968 for a description of Ellwood Pier and associated mussel populations) in that wave impact on the shore was much greater than that experienced on the pier pilings (Harger, 1967). At the outer end of the pier, under normal (non-storm) conditions, waves take the form of unbroken swells which rush past the pilings, creating a tremendous swirling and pushing, but little else. At the shore, on the other hand, all the kinetic energy contained in these swells is expended in the space of a few feet as the waves break. For this reason, and because measurement showed the shore to experience heavier wave action than the pier pilings (Harger, 1967) the former was classified as being more exposed than the latter.

To account for the presence of small *Mytilus edulis* only on the shore, I supposed that wave action either limited growth of the mussels such that individuals would not exceed 4 cm in length, or that the force of the waves simply removed any larger than this. (The maximum size attained by *M. edulis* within clumps attached to Ellwood Pier is 8 - 9 cm).

The following experiment was designed to investigate the problem. Artificial clumps of mussels were set out on the sea shore by confining individuals inside rectangular hardware-cloth cages ($\frac{1}{2}$ inch [1.27 cm] mesh). The cages were screwed tightly to seaward rock faces, thus confining a one-mussel thick layer in such a way as to prevent individuals being washed around by wave action. After a period of 3 weeks the cages were removed, leaving the surviving mussels firmly attached by byssal threads to the rock surface. Three size classes of mussels were used – large (9 - 10 cm), medium (7 - 8 cm), and small (5 - 6 cm) – together with 3 treatment groups within each size class – pure *Mytilus californianus,* pure *M. edulis,* and a mixture containing equal proportions of both species. The treatments involving the smallest size class were replicated twice, whereas the medium and large sizes were represented by one sample per treatment. The mussels were marked and measured individually (see Harger, 1967 for a description of the marking method) before the experiment was initiated.

b. Relationship Between Species Composition and Population Survival

Carpinteria reef is an extensive outcropping of rock occurring south of the city of Santa Barbara. In profile, the reef presents a steep seaward face approximately 10 feet (3 m) high behind which, and depressed by about 3 feet (1 m), the broad mass of the reef extends horizontally for a distance of about 100 yards (92 m). Due to protection by the front face, and because the reef itself tends to be flat, wave impact over the top of the rock is much reduced. Certainly the area is less exposed than Ellwood Shore.

During December, 1965, an intense storm was experienced in the Santa Barbara area. Prior to the storm the surface of Carpinteria reef was largely dominated by a thick sheet of mussels comprised mainly of *Mytilus edulis.* The storm stripped most of these animals from the reef and drastically altered the composition of the mussels in the remaining clumps. Areas within the original bed which were comprised principally of *M. edulis* were the ones lost, leaving groups composed mainly of *M. californianus.*

Table 1 indicates the relative proportions of the 2 species commonly present within the original mussel population as well as the highest proportions of *Mytilus edulis* which could be found after the storm. The proportion of *M. edulis* to *M. californianus* in the samples collected after the storm was much lower than in those collected before.

Table 1

Proportion of *Mytilus edulis* within natural beds of mussels at Carpinteria Reef before and immediately after a severe storm in December, 1965

	N	Proportion of *Mytilus edulis*
Before storm, December 1965	530	94%
	400	93%
After storm, December 1965	293	40%
	267	30%
	308	55%

The ratio of the component species within a clump, then, seems to have considerable importance in determining the resultant clump stability. To investigate this hypothesis a series of artificial mussel clumps was constructed containing the 2 species of mussels in the following proportions: *Mytilus californianus* to *M. edulis* – 1.0 : 0.0; 0.33 : 0.66; 0.5 : 0:5; 0.66 : 0.33; and finally 0.0 : 1.0.

Each ratio was represented by 3 separate clumps, one of which was comprised of small mussels (4 - 5 cm), the second of medium-sized mussels (6 - 7 cm), and the third of large mussels (9 - 10 cm). As far as possible, the mass of each clump was kept at about 1250 gr except for clumps of small mussels which averaged 600 gr.

Mussels forming each clump were placed in cheesecloth bags through the center of which was inserted a 20-inch (50 cm) length of 3-inch (7.6 cm) by $\frac{1}{2}$-inch (1.2 cm) redwood stake. The bag was then tied and stapled securely to the top and bottom of the stake in such a way that the mussels were pressed firmly against each other and against the center (Figure 1). An iron weight was lashed to the top end of the stake to insure the clump would not float in the water and each assemblage was suspended from a cross girder on Ellwood pier so that it hung just below low water.

RESULTS

The results of the experiment conducted on Ellwood shore are presented as survival curves in Figures 2, 3, and 4. Populations of pure *Mytilus californianus* survived well in

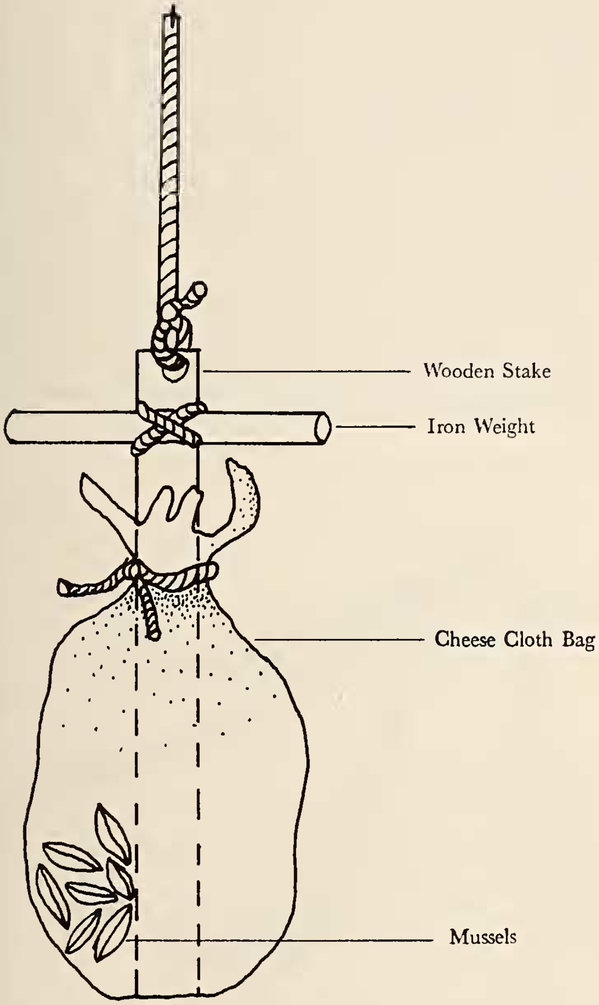

Figure 1

Artificial mussel clump constructed inside cheesecloth bag

all 3 size classes, whereas populations of pure *M. edulis* suffered highest mortality. Large *M. edulis* survived for less than 2 weeks before the animals were ripped from the rock face and pounded to pieces prior to removal of the cage. Medium-sized *M. edulis* fared a little better, lasting for 3 months before the last individual was dislodged. Small *M. edulis* lasted for 5 months and were finally eliminated through snail predation (*Thais emarginata* (DESHAYES, 1839) and *Acanthina spirata* (BLAINVILLE, 1832)).

Survival of the mixed populations was consistent for all 3 size classes. In each case, individuals of *Mytilus californianus* from the mixed populations disappeared faster than from populations of *M. californianus* growing alone. For the large and medium size classes, the survival of *M. edulis* was improved as a result of association with *M. californianus*. Survival amongst the small mussels, however, was not improved, probably because the principal mortality factor operating on these mussels was predation by the

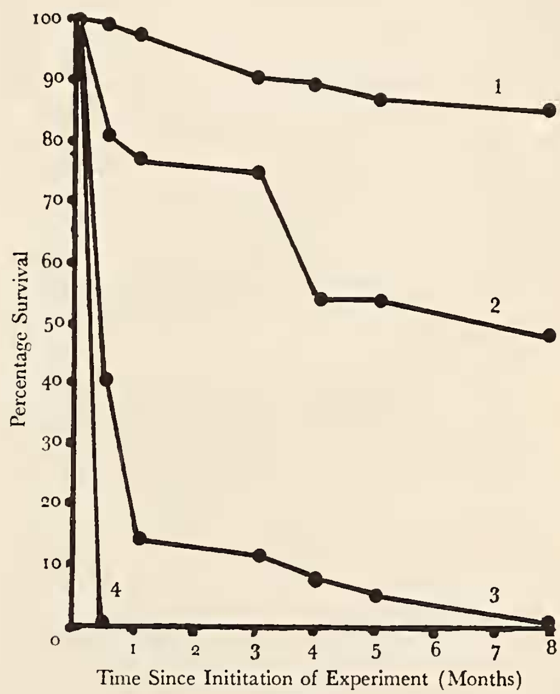

Figure 2

Survival curves of large mussels (8 - 10 cm) on Ellwood Shore Curve 1 represents *Mytilus californianus* alone. Curve 2 represents *Mytilus californianus* growing in association with *Mytilus edulis*. Curve 3, *Mytilus edulis* growing in association with *Mytilus californianus*, and Curve 4, *Mytilus edulis* alone.
Curves 2 and 3 were obtained from mussels growing in the same clump. Each clump originally contained 100 mussels. The experiment was started in January, 1966

carnivorous snail *Thais emarginata*, not wave impact. Both medium (7 - 8 cm) and small (5 - 6 cm) *M. edulis* showed growth over the period as did all classes of *M. californianus*.

This experiment indicates, among other things, that the safe upper size limit for *Mytilus edulis* in an exposed location depends to some extent on the presence of *M. californianus*. It is logical to assume that this upper limit will vary in accordance with amount of exposure, *i. e.*, wave impact.

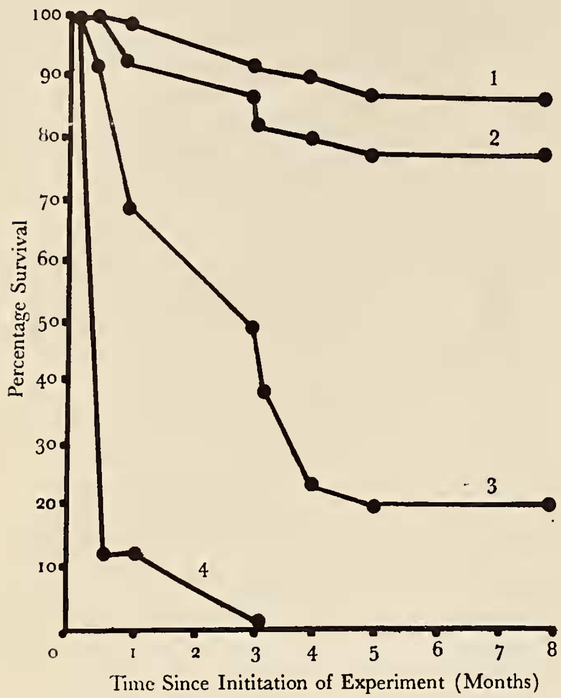

Figure 3

Survival curves of medium mussels (5 - 6 cm) on Ellwood Shore Curve 1 represents *Mytilus californianus* alone. Curve 2 represents *Mytilus californianus* growing in association with *Mytilus edulis,* Curve 3 *Mytilus edulis* growing in association with *Mytilus californianus,* and Curve 4, *Mytilus edulis* alone.
Curves 2 and 3 were obtained from mussels growing in the same clump. Each clump originally contained 78 mussels

As has been previously stated, the upper size limit for *Mytilus edulis* occurring in clumps at Ellwood pier is 8 - 9 cm. Larger individuals (up to 15 cm) can however be found growing in clumps of mussels attached below the low tide level to zinc electrode cables, which do not touch the sea floor. Such clumps are consequently protected from wave action and are at the same time not susceptible to predation by starfish (*Pisaster ochraceus* (Brandt, 1835) or *P. giganteus* (Stimpson 1857)), which occur beneath the pier (Landenberger, 1967).

A large sample of mussel shells gathered from the sea bed directly below the pier contained no *Mytilus edulis* larger than 7 cm. This perhaps indicates that wave action tends to dislodge this species from clumps formed in the intertidal region of the pilings once this size is reached.

The experiment utilizing artificial clumps at Ellwood Pier yielded the following results.

After 2 weeks the cloth bags rotted away and exposed the clumps to wave action, between March, 1966 to May, 1966. During this time the weather was mild with no severe winds. At the end of this period the clumps were taken in and the numbers of individuals of each species present recorded. Figure 5 indicates that clumps which had contained a high proportion of *Mytilus edulis* lost a high proportion of mussels. No difference due to size was apparent. This last result is a little surprising since clumps containing only small *M. edulis* (3 - 4 cm) can frequently be found growing on projecting pieces of iron, broken electrode cables, etc. Such clumps are usually broken up by wave action when the mussels reach 4 - 5 cm in length. This leads to the conclusion that the artificial clumps were not as firmly formed as natural associations would have been.

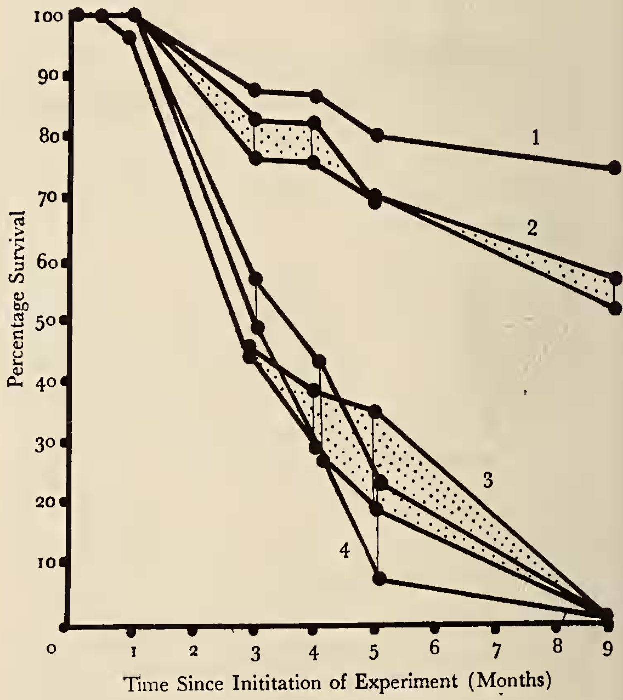

Figure 4

Survival curves of small mussels (3 - 4 cm) on Ellwood Shore Curve 1 (two replicates) represents *Mytilus californianus* alone. Curve 2 (two replicates) represents *Mytilus californianus* growing in association with *Mytilus edulis,* Curve 3, (2 replicates), *Mytilus edulis* growing in association with *Mytilus californianus,* and Curve 4 (2 replicates) *Mytilus edulis* alone
Curves 2 and 3 were obtained from the same two clumps. Each clump originally contained 68 mussels

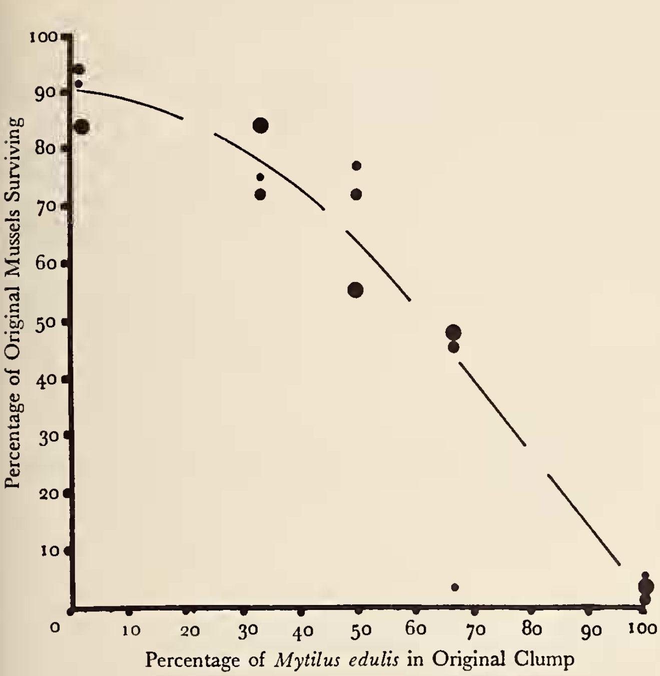

Figure 5

Relationship between the proportion of *Mytilus edulis* in the original artificial "cheesecloth" clumps and survival of both species (*i. e., Mytilus edulis* and *Mytilus californianus*). The clumps were suspended at Ellwood Pier, below low water, from March, 1966 until May, 1966. Small dots represent small mussels (4 - 5 cm) from original clumps comprised of 60 individuals. Medium dots represent "medium mussels" (6 - 7 cm) from original clumps containing 48 individuals. Large dots represent large animals (8 - 9 cm) from original clumps containing 24 individuals

The following conclusions emerge from these 2 exposure experiments:

1. Clumps of *Mytilus californianus* containing *M. edulis* are "weaker" than are similar clumps comprised only of *M. californianus.*

2. Survival of *Mytilus edulis* is increased in regions experiencing heavy wave impact if individuals of *M. californianus* are also present (this protection undoubtedly is a result of the stronger web of byssal threads which *M. californianus* weaves; *M. edulis* weakens this web wherever it occurs within a mixed species mat).

3. Small individuals of *Mytilus edulis* are better able to withstand the forces resulting from wave impact than are larger animals.

4. *Mytilus californianus* survives strong wave impact at all sizes.

The last two points are supported by the fact that small specimens of *Mytilus edulis* are able to attach to rocks almost as strongly as similar-sized *M. californianus.* Individuals longer than 5 cm, however, are more weakly attached than *M. californianus* of equivalent size (Harger, 1967).

DISCUSSION

From the foregoing evidence it seems reasonable to conclude that the effect a storm has on a population consisting of both *Mytilus edulis* and *M. californianus* depends on both the proportional representation of the two species and the size of the constituent individuals. Since clumps are progressively weakened by an increasing concentration of *M. edulis,* it follows that populations wherein this species is numerically dominant (over *M. californianus*) will be most susceptible to wave action.

In the Santa Barbara region heavy storms occur only during winter months, but they do not occur each year. It is thus possible for *Mytilus edulis* to build up heavy populations in protected and semiprotected regions (Ellwood Pier pilings and Carpinteria reef). Such populations usually flourish at the expense of *M. californianus* since *M. edulis* individuals always maneuver themselves so as to cover their competitors (Harger, 1968). In extremely quiet situations this results in the underlying *M. californianus* being smothered by silt. In areas, such as Carpinteria reef, large amounts of sand become deposited amongst the mussels with essentially the same effect; underlying mussels are smothered by oxygen-poor, heavily reduced material. This characteristic also adds to the progressive deterioration in clump stability caused by dominance and subsequent growth of *M. edulis.* Inclement weather may then eliminate large areas of *M. edulis,* leaving only *M. californianus*-dominated populations and juvenile *M. edulis. Mytilus edulis* is never entirely eliminated from such situations because the extreme spatial heterogeneity of the intertidal region ensures that some areas, behind rocks, etc., are always protected from direct wave action and, in addition, the juvenile mussels are capable of withstanding heavy seas (I have found small (2 - 3 cm) *M. edulis* growing in the intertidal region at Point Mugu, Ventura County, California, an external exposed region).

Areas stripped of mussels by storm action are soon colonized by barnacles and small mussels (particularly *Mytilus edulis*), thus setting the cycle in motion again.

The balance between the 2 species is interesting because the presence of *Mytilus californianus* seems always to enhance survival of *M. edulis* in the face of wave action. The growth pattern of *M. californianus* is, however, such that if *M. edulis* does not succeed in smothering its competitor at an early stage, it is itself incorporated into the clump matrix and crushed (HARGER, 1967). As far as *M. californianus* is concerned, the presence of *M. edulis* always serves to weaken the clump structure.

In conclusion, it seems evident that the effect a storm has on mussel populations (of any particular size) varies according to the proportions of the 2 species making up the association.

ACKNOWLEDGMENT

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CORRECTION

Figures 6 and 10 were inadvertently mutually misplaced on pages 49 and 52, respectively, in the article by the same author, published in no. 1 of the current volume. We apologize for any inconvenience this may have caused.

The Editor.